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The Radula and Penial Style of *Alderia modesta* (Lovén, 1844) (Opisthobranchia: Ascoglossa) from Populations in North America and Europe

by

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Abstract. Radulae and penial styles of *Alderia modesta* (Opisthobranchia: Ascoglossa), collected in Europe and on Pacific and Atlantic coasts of North America, were examined using light and scanning electron microscopes. There was no evident endemism in spite of geographic distances. Teeth from 81 specimens were counted and measured, and revealed considerable variation within size classes. On an individual basis, total number of teeth varied from 17 to 43; number of teeth in the ascending limb from 3 to 7; number in the descending limb from 5 to 19; and number in the ascus from 1 to 32. Ultrastructural details revealed by SEM photographs of teeth and penial styles indicated the inadequacy of most diagrams available in the literature.

INTRODUCTION

The order Ascoglossa (=Sacoglossa) is an assemblage of about 200 species of opisthobranch mollusks which feed by piercing cell walls of marine algae or marine angiosperms and sucking out the cell sap (JENSEN, 1980). Their radula consists of but a single row of teeth, and as new teeth are added to the radular ribbon, older teeth are discarded into a unique storage sac, the ascus. JENSEN (1980) reviewed literature pertaining to the ascoglossan feeding apparatus and the various prey species categories. She noted that there are structural differences in radular teeth between genera and species, but that usually the examination of only one radula per species formed the basis for this information.

Each radula consists of an ascending row (dorsal limb) of teeth, a descending row (ventral limb) capped by the current single protruding piercing tooth (this is not a rasping radula), and an ascus sac which contains all previously produced teeth. There is, then, considerable potential for numerical variation within these three sub-units of the radula. Analysis of 230 radulae of *Elysia chlorotica* Gould, 1870 (RAYMOND & BLEAKNEY, 1987) demonstrated surprising numerical variation and revealed just how inadequate was the available information (summarized for that species in table 3 of JENSEN, 1980).

Alderia modesta (Lovén, 1844) is an unusual ascoglossan in that it is limited to tidal marshes and estuarine flats, is consequently amphibious, and is commonly found "basking in the sun" upon *Vaucheria* algal mats, its principal food, at substrate surface temperatures of 25.5°C (BLEAKNEY & MEYER, 1979). This sea slug exhibits nil variation in gross anatomy in spite of its exceptional latitudinal and longitudinal distribution: northern Norway to the Mediterranean, western Greenland to New Jersey, and British Columbia to California.

The purpose of this present study was to investigate geographic variation in the radula and penial style (the hypodermic insemination apparatus) of *Alderia modesta*. Radulae and penial styles from diverse geographic areas were examined by means of light microscopy and then examined further with a JEOL JSM-255 scanning electron microscope. However, in order to discuss variation in the fine anatomy of these two organs, the illustrations presently available in the literature must be modified somewhat. A, B and C of Figure 1 depict attempts by three different authors to represent one radular tooth. Only the drawings by EVANS (1953) convey the basic anatomy, but only an SEM could provide the ultrastructural detail (Figures 1D–G) needed for the present comparative study. In Figure 2, the three-dimensional twist configuration of the tip of the spine of the penetrant style (Figure 2C) and the imbricated scales along the inner curvature (Figures 2D, E), were only revealed through SEM techniques.

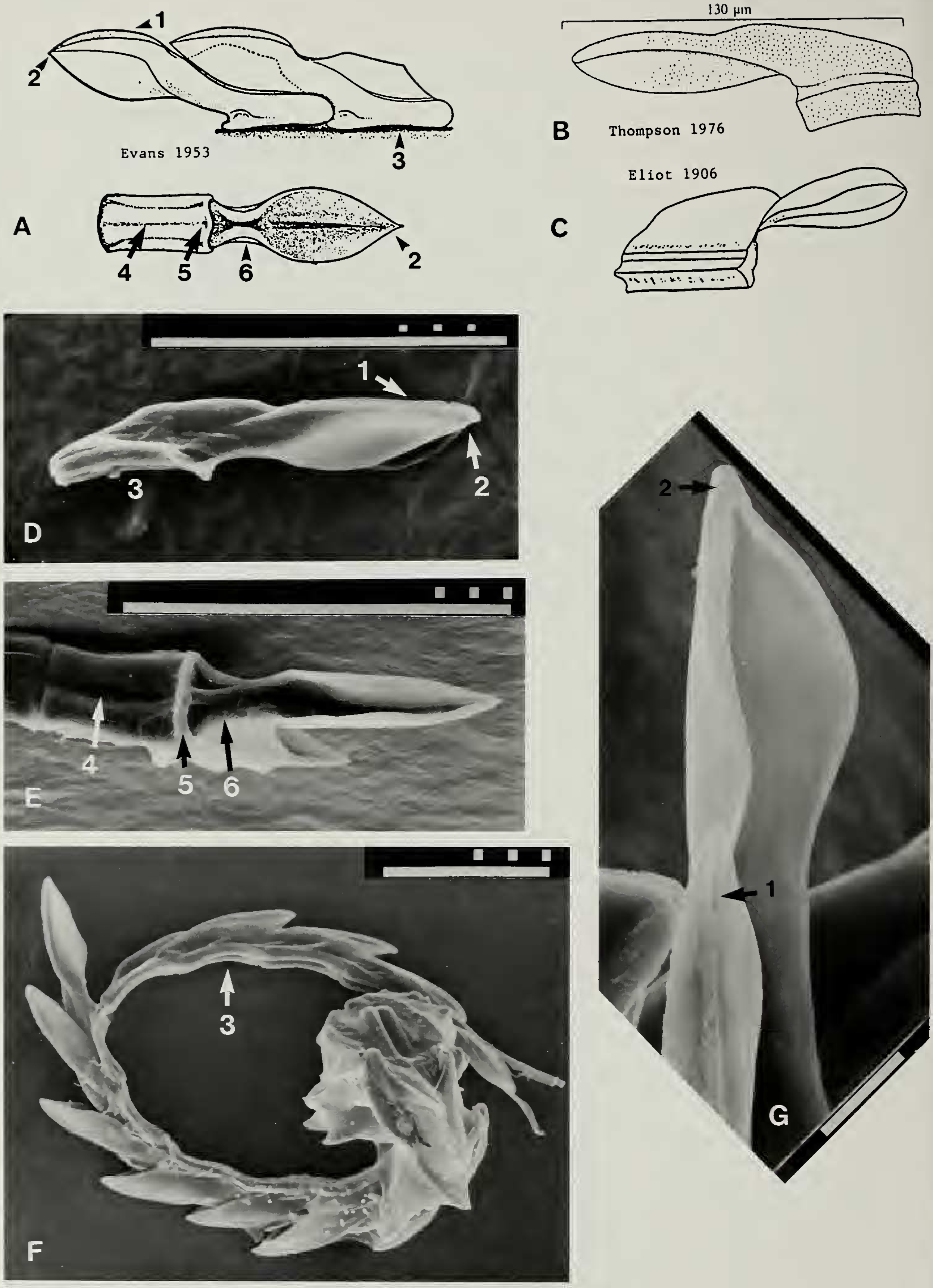
MATERIALS AND METHODS

With the exception of the Danish specimens supplied by Dr. Kathe R. Jensen, all specimens were collected by the

Table 1

Numbers of radular teeth in *Alderia modesta* relative to body length, from seven different geographic regions. BC = British Columbia; W = Washington; NS = Nova Scotia; NF = Newfoundland; P = Pool Hrb., England; N = Norfolk, England; D = Denmark. Radular teeth lost during preparation procedures are designated *. The symbol / in the ascus columns indicates that the descending tooth row continued uninterrupted into the ascus as a coil.

Body length (mm)	Ascending tooth row							Descending tooth row							Teeth in ascus							Tooth total						
	BC	W	NS	NF	P	N	D	BC	W	NS	NF	P	N	D	BC	W	NS	NF	P	N	D	BC	W	NS	NF	P	N	D
12			4							7							15							26				
(*n* = 2)			4							10							14							28				
10			4							9							10							23				
(*n* = 2)			5							11							9							25				
9							6							9							21							36
(*n* = 2)							4							15							3							22
8			5							16							/							21				
(*n* = 2)			5							19							/							24				
		5	5				5		7	7				10		11	15				9		23	27				24
7		4	5				4		6	8				12		*	14				3		*	22				19
(*n* = 10)		4	5						9	6						12	11						25	22				
			6							5							27							38				
			5							18														23				
	4	5	4				4	7	9	7				12	*	9	10				4	*	23	21				20
	5							7							*							*						
6	5							6							32							43						
(*n* = 9)	5							6							16							27						
	4							6							14							24						
	5							6							16							27						
	4	4	5	5	4		4	6	9	6	5	7		12	10	8	*	25	7		1	20	21	*	35	18		17
	5	4	4	4	6		5	5	15	6	6	7		12	16	/	17	22	12		3	23	19	27	32	25		20
5	6	4	5	5	5			7	7	15	6	6			22	13	/	29	13			35	24	20	40	24		
(*n* = 21)			4		5					15		7					/		8					19		20		
					4							7							9							20		
					5							6							10							21		
	4	4	4	4	5	5		7	16	15	6	7	5		26	/	/	20	10	27		37	20	19	30	22	37	
4	5	5	4	4	4	5		6	14	15	7	8	6		14	/	/	10	7	24		25	19	19	21	19	35	
(*n* = 20)	4	5	5	4		6		6	7	6	11		7		10	7	*	6		18		20	19	*	21	19	35	
				3		5					8		9					10		20					21		34	
						4							5							27							36	
			4	4	4	6				14	5	15	6				/	21	14	24				18	30	33	36	
3			4	4	5	5				14	6	6	7				/	14	14	22				18	24	25	34	
(*n* = 13)			4	4		4				14	5		5				/	12		30				18	21		39	
						7							7							24							38	
						5							6							23							34	
Total *n* = 81	Range: 3-7							Range: 5-19							Range: 1-32							Range: 17-43						



130 µm
Evans 1953
Thompson 1976
Eliot 1906
A
B
C
D
E
F
G
1
2
3
4
5
6

author. The localities, collecting dates, and the number of specimens from those samples utilized for radular tooth counts were (from west to east): (1) British Columbia, Vancouver Island, Bamfield Marine Station, August 1980 ($n = 12$); (2) Washington State, San Juan Island, Friday Harbour Laboratories, September 1980 ($n = 10$); (3) Nova Scotia, Minas Basin, 1966, 1969, 1975, 1976, 1982, 1985 ($n = 22$); (4) Newfoundland, Parsons Pond (northwest coast), August 1985 ($n = 10$); (5) England, Pool Harbour, June 1979 ($n = 10$); (6) England, Norfolk, Burnan Deepdale, June 1980 ($n = 10$); and (7) Denmark, Resund, Averre Beach, October 1964 ($n = 7$).

Although body length of *Alderia modesta* ranged from 3 to 12 mm, only 8 specimens exceeded 7 mm. Table 1 is a compilation of body length, geographic origin, and numbers of teeth in ascending limb, descending limb, ascus, and total.

In addition to the above 81 specimens, others were examined, photomicrographs taken, and still others were dissected for their radulae and penial styles and these were mounted for SEM examination. The techniques employed were described previously in BLEAKNEY (1982) and in RAYMOND & BLEAKNEY (1987) and involve dissociation of tissues by Beckman Tissue Solubilizer #450 (BTS-450). SEM mounts were made of radulae from British Columbia ($n = 4$), Nova Scotia ($n = 2$), Newfoundland ($n = 1$), and England ($n = 3$). Penial styles were prepared for SEM from all sites except Norfolk: British Columbia ($n = 3$), Washington ($n = 5$), Nova Scotia ($n = 5$), Newfoundland ($n = 2$), England ($n = 1$), and Denmark ($n = 2$).

Also recorded was the length of the base and the cusp of the single feeding tooth in each radula, in hopes of finding regional differences in that ratio.

To illustrate ontogenetic changes in tooth shape, and to record the one minor geographic variation noticed, each tooth in an entire radular series was measured for a specimen from Washington and from Denmark and these data are summarized in Table 2 and Figure 9.

RESULTS

There was remarkably little variation from population to population and certainly no indication of geographic differences that warrant taxonomic consideration, in this writer's opinion. The highest ascus tooth counts fell to Newfoundland and Norfolk, as much as double that of other areas. In the various categories of tooth counts, and for incidence of coiled radular ribbon, the Washington sample was similar to Nova Scotia, not adjacent British Columbia. Admittedly, the sample sizes were small, but columns of figures in Table 1 are encouragingly consistent within each sample.

Numbers of Teeth

Considering the entire sample of 81 radulae, it is evident that for *Alderia modesta*:

(1) The number of ascending teeth rarely deviates from 4 or 5, with a range of 3 to 7.
(2) The number of descending teeth is more difficult to delimit because the older teeth may quickly separate from the ribbon and form a jumble in the ascus or they may remain attached for a longer period and form an extended row (Figure 3), or may never detach and thus form a continuous coil, housed in the ascus (Figure 4). Only Washington and Nova Scotia samples had individuals with completely coiled tooth complements. The usual number of descending teeth is 6 or 7, but does range from 5 to 19. Series of 9 or more connected descending teeth were common in samples from Washington (6 of 10), Nova Scotia (13 of 21), and Denmark (7 of 7). Only the British Columbia sample lacked the long coiled radula.
(3) The number of loose teeth packed in the ascus sac varied from 1 to 32, and reflected the degree of persistence of the radular ribbon with attached teeth. There is considerable individual variation evident, but at the regional level the highest counts were British Columbia (32), Norfolk (30), and Newfoundland (29). However, the highest counts relative to other samples in the same size classes were the 3-mm class from Norfolk and the 5-mm class from Newfoundland, which were often double the number of teeth (Table 1).
(4) The highest individual total number of teeth was 43 from British Columbia, but Norfolk had the most individuals with totals exceeding 30 teeth. The range for the 81 specimens was 17 to 43.

When comparisons were made between size classes from the same locality, there was often little relationship between body length and total number of teeth. Nova Scotia

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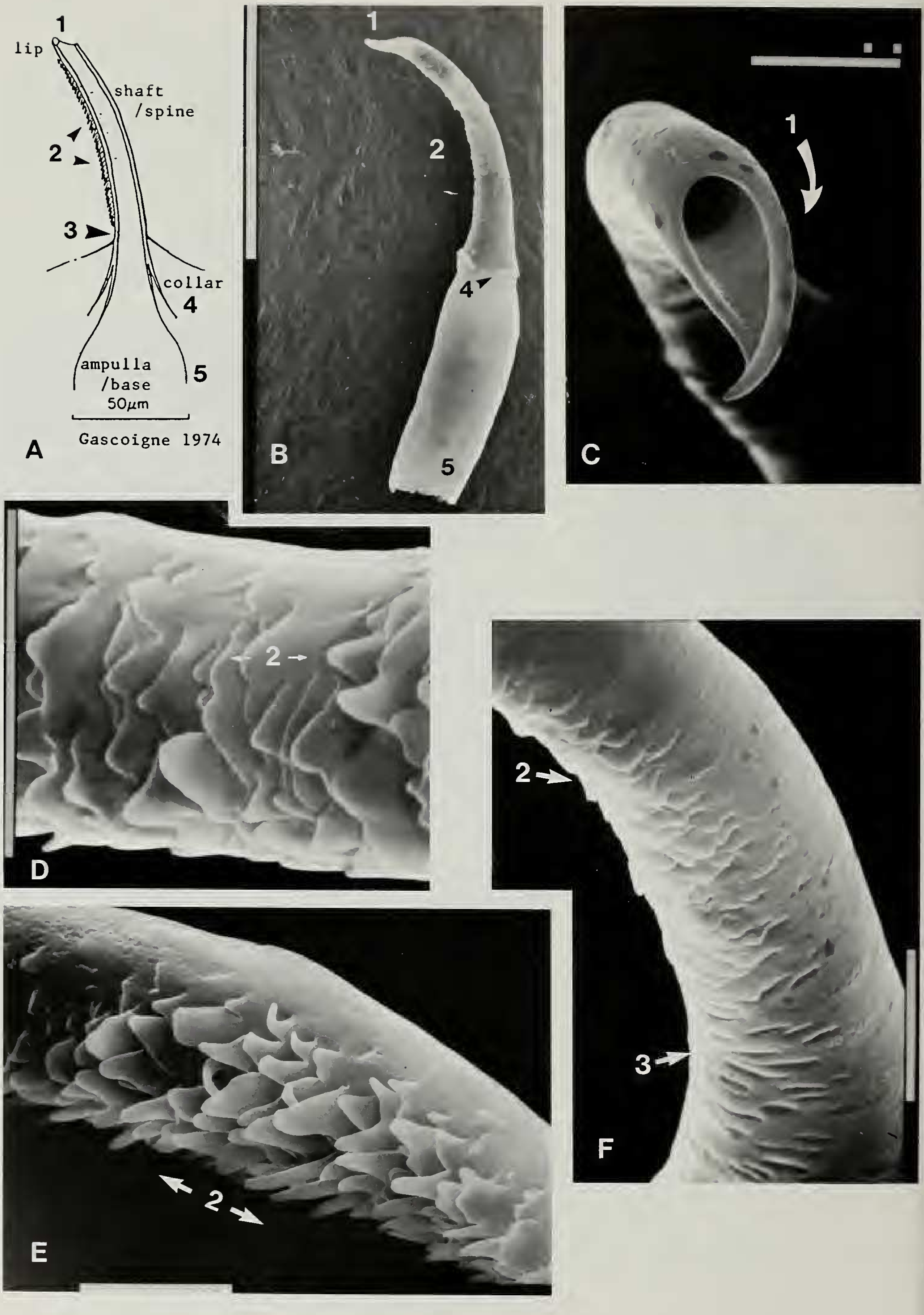
Figure 1

A–C. Diagrams of radular teeth of *Alderia modesta* reproduced from the literature (A, from EVANS, 1953; B, from THOMPSON, 1976; C, from ELIOT, 1906) with comparative SEM micrographs (D–G) indicating six features of these diagrams which are inaccurate: (1) there is a narrow dorsal keel on the cusp; (2) there is a slightly hooked but blunt tip on the cusp; (3) the tooth base, from lateral aspect, is definitely concave; (4) the tooth base has a deep ventral trough; (5) the tooth base is bordered anteriorly by a prominent transverse ridge; (6) the base of the cusp, ventral aspect, has 3 not 2 ridges. D is from Newfoundland; E is ventral aspect of spatulate tooth, base and cusp from Norfolk, England; F is entire radula with ascus, body length 4 mm, Norfolk; G is cusp portion of two teeth, dorsal and ventrolateral aspects, from Nova Scotia. Bar scales of D, E, and F equal 100 μm, and the scale in G is 10 μm.


1
lip
shaft
/spine
2
3
collar
4
ampulla
/base
5
50µm
Gascoigne 1974
A
B
C
D
E
F

animals of 5 mm can have tooth counts equal to 12-mm specimens. Comparing different localities is even more striking. For example, some 3-mm Norfolk specimens have double the tooth count of 3-mm Nova Scotia specimens, and have as much as 1.5 times the number of teeth as the 12-mm Nova Scotia size classes (Table 1).

Shape and Size of Teeth

The individual teeth of *Alderia modesta* are essentially identical throughout the species' range. There are four preliminary teeth; the first is nearly triangular, the second is rectangular, the third has a rectangular base with a short spike, and the fourth is the first tooth to possess the long spatulate cusp (Figures 5–7). The cusp becomes relatively larger in the fifth and succeeding teeth. The ontogenetic change in base-cusp ratio is evident in Table 2 and Figure 9, and the two examples chosen represent the extremes observed in this study. Only the Danish specimens had these relatively larger tooth bases, and this was most pronounced in the youngest teeth. At the 8th tooth the base-cusp ratio of the two samples converges and continues in parallel (Figure 9) even though the Danish teeth are larger. The two specimens selected for Table 2 had the continuous coiled radular ribbon and thus all the teeth were in their original sequence. Each was measured although only every second tooth is listed in Table 2.

The base-cusp ratio of the single projecting feeding tooth (Figures 4, 5) in 70 specimens varied from 1.12 to 2.1, but this range had been reached at body lengths of only 4 and 5 mm. In fact, 11 specimens in the 4- to 6-mm size class had ratios of 1.9 to 2.1 which equalled or exceeded the base-cusp ratio of larger 10- to 12-mm size classes. All but 9 specimens were within ratios of 1.5 to 1.9, and no geographic differences were evident.

The length of the largest feeding tooth recorded from each locality is listed in Table 3 under body length classes. The size range of that same tooth within the 3-mm body length is also listed and serves to emphasize once again the surprising extent of individual variation and the equally surprising paucity of evident geographic races derived from the potential within that variation.

There is, however, one peculiar relationship evident in Table 3, and that is between tooth maximum and the year in which the specimens were collected. The largest teeth (over 200 μm) are from the 1960s, the smallest (near 135 μm) from 1979–1980, and the intermediates (at 157 μm) from 1985. In light of RAYMOND & BLEAKNEY's (1987) discovery of annual fluctations in tooth production in *Elysia chlorotica*, the above "coincidence" regarding tooth size may have some validity.

Penial Style

Examination of penial style morphology by light microscopy indicated no differences from one population to another (Figure 8) and, therefore, geographic comparisons were not attempted. There were, however, size differences associated with increased body length which indicate that this structure, unlike the teeth, is either continually being restructured (length and diameter) or is periodically discarded and renewed. These data, with information from the literature, are summarized in Table 4.

Two ultrastructural features were examined with the SEM in hope of detecting geographic differences. The first was the curl of the penetrant tip of the style (Figure 2C). No variation was evident. Using light microscopy, GASCOIGNE (1974) reported this curled point as merely a thickened edge at one side of the orifice (Figure 2A).

The second feature examined was the scaly surface of the inner curvature of the spine and in this case a minor "variant" was noted in the longer scales of the Newfoundland samples (Figure 2E). This may or may not be a constant feature of west coast Newfoundland populations. GASCOIGNE (1974, 1976) understandably concluded these scales were spinules and first reported them as occurring in a narrow band (1974) and later (1976) as arranged in a single row. His diagram (reproduced here as Figure 2A) omitted much of the inflated basal cylinder (Figures 2B, 8). Not previously reported in the literature are the pits and slits at the base of the style spine (Figure 2F). These vary in size, shape and depth, but again individual variation negated any hope of discovery of a region exhibiting distinct endemism.

DISCUSSION

JENSEN (1980: table 4) indicated that no information was then available on the numbers and size of *Alderia modesta* teeth, even though she cited EVANS (1953) in which his fig. 2 has a tooth formula of 4/7 plus ascus, and a stated feeding tooth length of 135 μm. Evan's measurements agree well with the present study. THOMPSON (1976) reported tooth counts of 20 and 16 but did not indicate how many in the ascending and descending series. His specimen with 16 teeth was 3 mm long and had 9 worn teeth in the ascus, an unusually low ascus count (Table 1).

The basic anatomy of the buccal mass and of the radular

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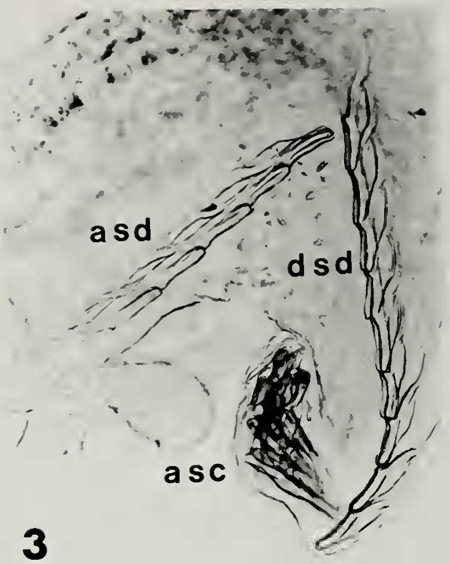
Figure 2

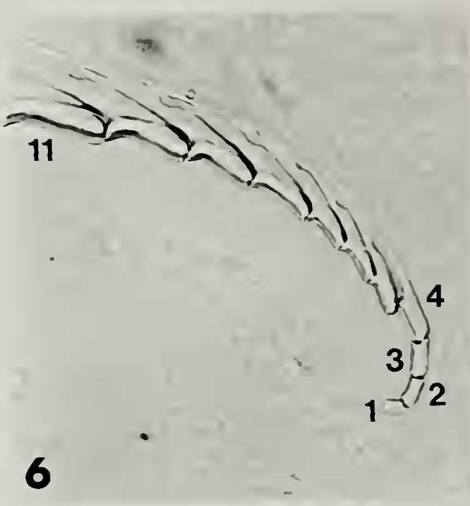
A. Diagram of penial style of *Alderia modesta* from GASCOIGNE (1974). B–G. SEM micrographs illustrating finer details: B is from Nova Scotia, note relative size of base; C is the penetrant tip of a 7-mm specimen, Nova Scotia; D is imbricated scales on inner curvature of spine, Nova Scotia; E is typical of Newfoundland samples; F is basal area of spine showing pits and grooves noted in all samples, this one from Washington. Scale bar in B represents 100 μm; in C–F, bar is 10 μm.



3

4

5



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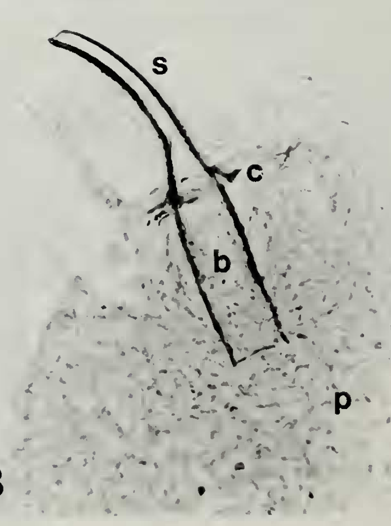

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Table 2

Base-cusp lengths in μ and their ratios, of a series of teeth from one Danish 7-mm specimen and from one 5-mm Washington State *Alderia modesta.* Each possessed 18 teeth and the 15th was the projecting feeding tooth. Of the seven populations sampled, only the Danish slugs had such large tooth bases.

Tooth no. in series	Denmark Tooth length Base	Cusp	Total	B-C ratio	Washington State Tooth length Base	Cusp	Total	B-C ratio
4	18.0	22.5	40.5	1.25	9.0	27.0	36.0	3.0
6	22.5	31.5	54.0	1.4	13.5	34.0	47.0	2.5
8	22.5	45.0	67.5	2.0	18.0	36.0	54.0	2.0
10	31.5	58.5	90.0	1.85	22.5	45.0	67.5	2.0
12	40.5	76.5	117.0	1.88	29.0	54.0	83.0	1.8
14	54.0	99.0	153.0	1.83	36.0	65.0	101.0	1.8
15f	63.0	99.0	162.0	1.57	36.0	67.5	103.5	1.9
16	63.0	103.5	166.5	1.64	45.0	72.0	117.0	1.6
18	76.5	121.5	198.0	1.58	45.0	79.0	124.0	1.75

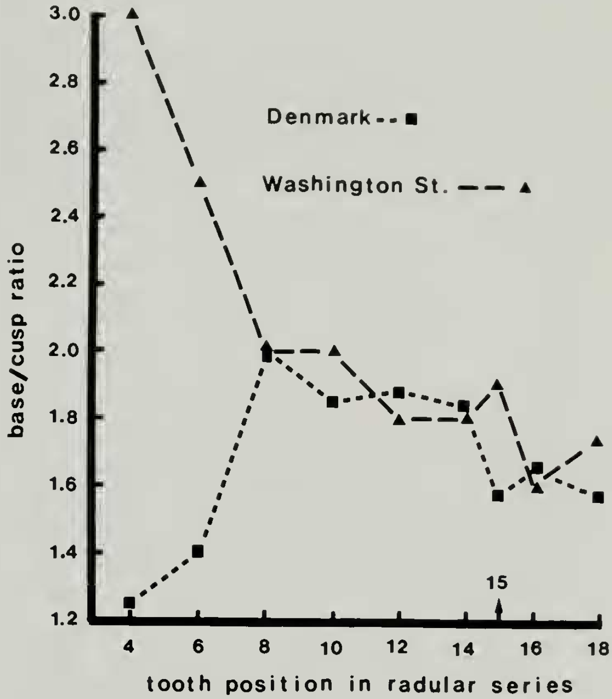

Figure 9

Plot of data in Table 2 showing the extreme initial difference in base-cusp ratio and the rapid convergence to a common pattern.

teeth (Figure 1A) depicted so well by EVANS (1953), lacks only the finer details that SEM photographs can provide. These SEM anatomical refinements are assembled in Figures 1D–G, with the Evans drawings, and are: (1) narrow dorsal keel on cusp; (2) slightly hooked, but blunt tip on cusp; (3) base of tooth, lateral aspect, has a concave curvature; (4) base of tooth, ventral aspect, has a deep central trough; (5) base of tooth, ventral aspect is bordered anteriorly by a prominent transverse ridge; and (6) base of cusp, ventral aspect, has 3 not 2 ridges.

In spite of isolation between Atlantic and Pacific populations by both immense distances and time periods, distinct endemism is not evident in these samples of *Alderia modesta.* Genetic continuity is an unlikely explanation, as the Central American continuity between Atlantic and Pacific oceans closed about 2.5 million years ago, and the potential trans-arctic marine connection has recently undergone successive glaciations. To postulate a recent contiguous series of low-salinity coastal marsh habitats, a requisite for the food alga (*Vaucheria*) of *Alderia* across the arctic from Greenland to Alaska is unnecessary if not unreasonable. In fact, this author would argue that the evidence is against recent gene flow even between Europe and eastern North America. Considering deciphered continental drift patterns, the North Atlantic basin at its inception (90–70 million years ago) undoubtedly was a single faunal unit. The gradual distancing of those eastern and western shores has effectively separated the gene pools of

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Explanation of Figures 3 to 8

Figure 3. Buccal mass with radula from 9-mm specimen of *Alderia modesta,* Denmark. Asd indicates ascending (dorsal) row of radula, dsd is descending (ventral) row with 9 teeth attached to the radular ribbon, whereas all previously formed teeth have detached and are packed into the ascus sac (asc).

Figure 4. Radula of 12-mm *A. modesta* from Nova Scotia, showing continuous coil of radular ribbon with retention of teeth in their original production sequence. The projecting piercing feeding tooth is indicated at f.

Figure 5. Descending series of 15 radular teeth from 4-mm *A. modesta,* Nova Scotia. Note 12 teeth with thick bases and long cusps, and the 3 small preliminary teeth (at arrow) without cusps. Feeding tooth is at f.

Figure 6. The first 11 teeth of a 4-mm *A. modesta,* Nova Scotia, showing dramatic morphological transition from tooth no. 3 to tooth no. 4, and the rapid increase in the mass of each subsequent tooth.

Figure 7. Part of ascus contents of 12-mm *A. modesta,* Nova Scotia, with the first 5 teeth numbered. Note the characteristic short spur on tooth no. 3 in contrast with the long cusp on tooth no. 4.

Figure 8. Typical penial style of *A. modesta* showing spine (s) protruding from top of large penis (p) in which the style base (b) with collar (c) is embedded. From a Danish specimen 6 mm in length.

Table 3

Length in μm of longest feeding tooth recorded for *Alderia modesta* from each geographic locality and the body length of that specimen. In the 3-mm body-length column, the entire range of sizes of the feeding tooth is listed. Note that the largest teeth are from 1960s populations, the smallest from 1979 to 1980.

	Body length (mm)							
Locality	3	4	5	6	7	9	12	Collection year
B.C.	—	—	—	135	—	—	—	1980
Wash.	—	—	—	—	135	—	—	1980
NS	108–153	—	216	—	238.5	—	225	1966, 1969
Nfd.	103–144	—	157.5	—	—	—	—	1985
Pool	76–135	—	135	—	—	—	—	1979
Norf.	99	130.5	—	—	—	—	—	1980
Denm.	—	—	—	—	—	202.5	—	1964

the two coasts, and it is evident that there has been ample time for speciation within these amphiatlantic genera, for at present only 64% of West Atlantic nudibranch species are amphiatlantic, and more strikingly, only two ascoglossan species of the seven species reported from the North American coast north of Cape Hatteras, also occur in Europe (FRANZ, 1970). If there were a transatlantic genome pipeline for benthic opisthobranchs, then many additional European estuarine and open coast species should occur on our Canadian shores, especially the ubiquitous intertidal genus *Limapontia* (with 3 species) which so often occurs in company with *Alderia modesta* in Europe. While arguing for genetic ultra-conservatism in *Alderia,* it is worth noting that *Placida dendritica* (Alder & Hancock, 1843) and the marsh anemone *Nematostella vectensis* (Stephenson, 1935) have a similar European and east-west coast of North America distribution, with no indication of speciation.

The potential, however, for some manifestation of genetic drift, mutations, and natural selection pressures is certainly there, as this species has a short life-span of perhaps 2 to 6 months (CLARK, 1975) and can lay an average of 1000 eggs/day during the warmer months, after maturing within 10 days of its post-veliger metamorphosis (SEELEMANN, 1967). Also, within the Ascoglossa, radulae and penial styles can and have evolved into a variety of morphs (GASCOIGNE & SARTORY, 1974). The minor degree of individual variation noted within my samples of *Alderia modesta* (tooth size, total number of teeth, coiled radula, penial scales) was enough to encourage this investigator to imagine that one or two of these minor features might possibly occur as a distinct characteristic in perhaps even one of these isolated populations. Only examination of larger samples over a period of several years might eventually reveal the following: (1) in Denmark (and Baltic region?) the radular ribbon always coils into the ascus; (2) in Newfoundland (and Greenland?) the penial scales are always long; and (3) along the Norfolk coast (and North Sea?) the rate of tooth production is always twice that of other regions. With more data it may become possible to demonstrate that these minor regional differences in tooth and penial morphology have restricted genetic latitude, whereas, absolute size and numerical differences fluctuate easily with an assortment of environmental parameters.

Perhaps the overall anatomical uniformity of *Alderia modesta* populations should not be surprising because it may be the only representative of the entire family Alderiidae (JENSEN, 1983). The atrophied heart, the random hypodermic insemination, the unusual Xanthophyta food, the highly amphibious habits, and so on, bespeak an exceptional history of adaptations. Perhaps *A. modesta* is an ancient genus from the base of the stiligerid line, as GASCOIGNE suggested (1985), and has survived the competition of more recent ascoglossan groups through its unique specializations. Comparison of the genome of *Alderia* with that of its antithesis the genus *Elysia* (with perhaps over 60 species) would add a valuable dimension to the recent significant series of discussion papers on evolution and adaptation within the Ascoglossa: GASCOIGNE (1976, 1985), CLARK & BUSACCA (1978), JENSEN (1980), and CLARK & DEFREESE (1987).

Table 4

Comparative lengths of penial styles of *Alderia modesta* relative to body length, from this study and the literature.

		Penial style length (μm)			
Locality	Body length (mm)	Base	Spine	Total	Source
Nova Scotia Newfoundland					
Nova Scotia	3	50	70	120	This study
California	4	75	100	175	This study
	5	89	100	189	This study
British Columbia	5.5*	—	—	180	HAND & STEINBERG, 1955
Washington	6	88	108	196	This study
State	7	100	125	225	This study
England	—	—	100	—	GASCOIGNE, 1974
England	—	—	120	—	GASCOIGNE, 1974

* An average.

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